

NOTES

CHARACTERISTICS OF SEEDLING ESTABLISHMENT OF *STENOCEREUS STELLATUS* (CACTACEAE) IN THE TEHUACÁN VALLEY, MEXICO

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ABSTRACT—Some characteristics of germination and seedling establishment of *Stenocereus stellatus*, a columnar cactus that has vegetative propagation and sexual reproduction, were determined through field and laboratory experiments with seeds collected at 2 sites. Germination and seedling establishment varied between sites. Seedling survivorship also was affected by solar radiation. Different intrinsic and extrinsic characteristics, such as genetic variation, seed predation, and rainfall, could affect the successful establishment of this species. Vegetative propagation might be a complementary mechanism to sexual reproduction that contributes to population persistence.

RESUMEN—Algunas características de la germinación y el establecimiento de plántulas de *Stenocereus stellatus*, un cactus columnar con propagación vegetativa y reproducción sexual, fueron determinadas a través de experimentos de campo y laboratorio con semillas colectadas en 2 sitios. La germinación y el establecimiento de plántulas variaron entre sitios. La sobrevivencia de las plántulas también fue afectada por la radiación solar. Diferentes características intrínsecas y extrínsecas como la variación genética, la depredación de las semillas y la lluvia pueden afectar el establecimiento exitoso de esta especie. La propagación vegetativa puede ser un mecanismo complementario a la reproducción sexual que contribuya al mantenimiento de la población.

Stenocereus stellatus is one of the few species of columnar cacti with 2 modes of regeneration, vegetative propagation and sexual reproduction (Godínez-Alvarez et al., 2003). Vegetative propagation occurs through stem segments that fall to the ground and develop their own roots, giving origin to new individuals. These new roots and stems are produced from meristematic regions of fallen stems mainly during the rainfall season. In relation to sexual reproduction, this species is hermaphroditic, producing its flowers and fruits from March to July and from August to September, respectively (Casas et al., 1997). Field observations to determine the relative importance of these processes indicated that sexually derived individuals were less common (0 to 33%) than those produced vegetatively (67 to 100%; Pérez,

2004). These estimates considered individuals derived from vegetative propagation and less than 0.5 m in height that were still joined to fallen branches of conspecific adults or had evidence of previous joints (Pérez, 2004). Field observations also suggested that vegetatively and sexually derived individuals apparently did not differ in the number of fruits per plant, nor in the number of seeds per fruit. Reproductive differences have been observed among individuals growing in different populations throughout its distribution. For instance, during 2002, individuals in one population (Zapotitlán) produced 18 ± 4 fruits ($n = 38$), whereas those in another population (Tilapa) only produced 5 ± 1 ($n = 10$; Pérez, 2004).

Different abiotic and biotic characteristics, such as shade, soil, and water, as well as seed

dispersers and predators, can affect the establishment of new individuals. Other intrinsic characteristics, including genetic variation among populations also can affect the probability of successful establishment of seedlings (Brum, 1973; Steenbergh and Lowe, 1977; Parker and Hamrick, 1992; Bowers, 1997; Godínez-Alvarez et al., 2003). The purpose of this study was to determine, through field and laboratory experiments, some characteristics of seed germination and seedling establishment of the columnar cactus *S. stellatus*.

This species of columnar cactus is endemic to central Mexico, where it inhabits the Tehuacán Valley and the southern portion of the Balsas River Basin in the Mexican states of Morelos, Puebla, Guerrero, and Oaxaca (Casas et al., 1997). In these regions, *S. stellatus* can occur in 3 populations: wild, cultivated, and managed in situ. Wild populations represent a permanent source of individuals with particular morphological traits that are transplanted by people to cultivated and managed populations (Casas et al., 1997, 1999a, 1999b). Maintenance of wild populations depends on sexual reproduction and vegetative propagation of individuals.

This study was conducted in 2 wild populations of *S. stellatus* located in the Tehuacán Valley, Zapotitlán (18°20'N, 97°28'W; 1,550 m a.s.l.) and Tilapa (18°09'N, 97°06'W; 910 m a.s.l.). Both sites have a semiarid climate with an average annual rainfall of 400 to 441 mm and a mean annual temperature of 21 to 24°C. In Zapotitlán, the main vegetation type is arid tropical scrub, where *Castela tortuosa*, *Cercidium praecox*, *Mimosa luisana*, *Myrtillocactus geometrizans*, and *Prosopis laevigata* are some of the dominant species. The main vegetation type in Tilapa is tropical deciduous forest dominated by *Bursera aptera*, *Ceiba parvifolia*, *Escontria chiotilla*, *Mimosa luisana*, and *Pachycereus weberi* (Valiente-Banuet et al., 2000). The management history of the 2 sites is unknown. However, based on field observations, it is assumed that modern management practices, such as grazing and gathering of firewood, fruits, and plants by local people, have affected both sites similarly.

During 2002, seed germination was analyzed in the laboratory and seedling survivorship was determined in the field. Thirteen to 25 mature fruits were collected from at least 10 plants

growing at each site and transported to the laboratory. For each site, seeds were obtained by dissection, pooled, and then divided into 8 replicates of 25 seeds each. Seeds were sown in Petri dishes with moistened filter paper and maintained in an environmental growth chamber (constant temperature of 25°C, fluorescent light, and 12-h photoperiod). Dishes were checked daily to record the number of germinated seeds. The criterion used to consider a seed germinated was radicle emergence. The proportion of germinated seeds at the end of the experiment and the rate of germination were analyzed with log-linear models.

With respect to survival, 250 seeds from each site were sown in a plastic container filled with soil obtained from the same field site where seeds were collected. For each site, 8 plastic containers were maintained for 10 days in the same conditions described for germination. After this period, seedlings were moved to the laboratory, where they remained for 31 days at ambient conditions of temperature and light. During the last 10 days prior to being transported to the field, seedlings were acclimatized by decreasing watering and increasing direct solar radiation. Seedlings from both sites were introduced only to the Tilapa site instead of their corresponding site of origin to avoid logistical problems. In the field, seedlings were placed in 2 settings to evaluate the possible effects of direct solar radiation on survivorship: 1) under the canopy of the shrub *Mimosa luisana*, and 2) in open spaces. For each setting, 4 replicates with 35 to 150 seedlings were transplanted and the number of surviving seedlings was recorded every 15 to 30 days. Data were analyzed with log-linear models.

Additional experiments were conducted at each site at the beginning of September 2003 to analyze seedling emergence and survival in the field. Seeds were collected in Zapotitlán and Tilapa one month before experiments were performed. The experimental design used was a 2 × 2 factorial in which seeds were sown in open spaces and beneath *M. luisana*, and in sites where predators were either excluded or non-excluded. Invertebrate and vertebrate predators were excluded with 12-mm wire mesh and natural resin. Each treatment consisted of 5 replicates with 100 seeds, and censuses were made every 15 to 20 days to re-

cord the number of emerged and surviving seedlings.

Results obtained in the experiments conducted during 2002 showed that the number of germinated seeds and the seedling survivorship varied between the seed populations from Zapotitlán and Tilapa. In relation to germination, there were differences in the rate and proportion of germinated seeds ($\chi^2 = 9.3$, $df = 1$, $P = 0.002$). Seeds obtained from plants growing in Tilapa germinated 2 days before those from Zapotitlán (Fig. 1a). However, at the end of the experiment, the rate and proportion of germinated seeds from Zapotitlán (rate: 0.91 seeds/day, proportion: 0.43 ± 0.06) were significantly higher than those for seeds from Tilapa (rate: 0.52 seeds/day, proportion: 0.28 ± 0.04). With respect to survivorship, seedlings were alive in all treatments after 160 days of the beginning of the experiment. Analysis of the survivorship curves indicated that the effect of site ($\chi^2 = 95.7$, $df = 1$, $P < 0.0001$) and interaction between solar radiation and time ($\chi^2 = 8.7$, $df = 1$, $P = 0.003$) were significant, explaining 31% and 3% of the total variance, respectively. Individuals from Zapotitlán had higher survivorship than those from Tilapa. Despite this fact, seedlings from both sites growing under the canopy of *M. luisana* survived better than those growing in open spaces (Fig. 1b). It is important to note that seedlings were transported only to Tilapa instead of their corresponding site of origin.

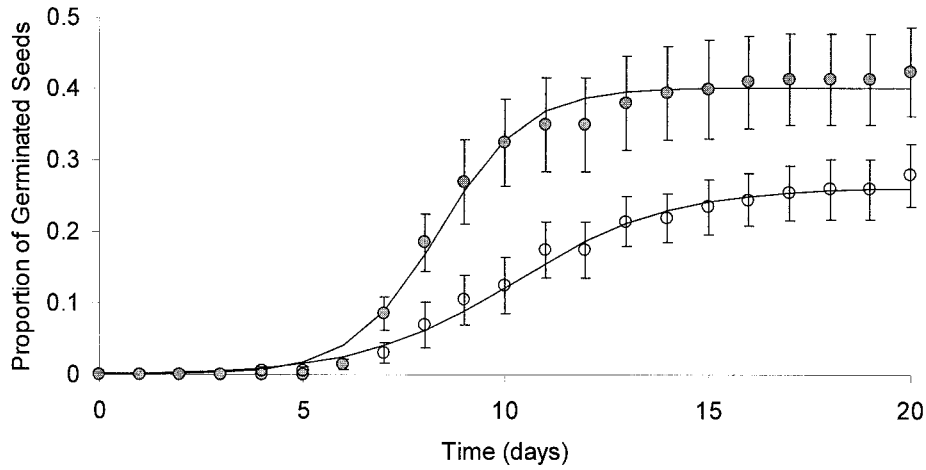
During 2003, germination of *S. stellatus* did not occur in any site due to seed predation and probably insufficient rainfall. Seeds in treatments that were not excluded from predators were immediately removed by the ants *Pogonomyrmex barbatus* and *Pheidole*. This high seed predation occurred similarly in open spaces and beneath the canopy of *M. luisana*. Seeds in the treatments where predators were excluded did not germinate. This result might be related to the rainfall pattern at Zapotitlán and Tilapa during the month (September) of this experiment. In both sites, the amount and frequency of rainfall decreased after seeds were sown in the field (Fig. 2c).

Seed germination and seedling establishment are 2 critical phases in the life cycle of desert plants. During these phases, high mortality rates occur due to several abiotic and biotic characteristics, including those character-

istics intrinsic to species (Brum, 1973; Steenbergh and Lowe, 1969, 1977; Parker and Hamrick, 1992; Bowers, 1997; Godínez-Alvarez et al., 2003). The evidence presented here suggests that the successful establishment of *S. stellatus* seedlings depends on the effects of different intrinsic and extrinsic characteristics. With respect to intrinsic characteristics, seed germination in the laboratory showed that there were significant differences between seeds from Zapotitlán and Tilapa. These differences might be related to genetic variation produced by the existing environmental conditions of each site, although there were no apparent differences in size, weight, and morphology of seeds. Genetic variation in seed germination could affect the probability of seedling establishment, depending upon the particular site where this process occurs. Seeds from Zapotitlán had higher rates and proportions of germination compared to seeds from Tilapa. In addition, it has been suggested that seeds of *S. stellatus* need an after-ripening period to increase their germination percentage (Rojas-Aréchiga et al., 2001).

In relation to extrinsic factors, our results suggest that solar radiation, seed predation, and rainfall also could limit the seedling establishment of *S. stellatus*. Seedlings grown under the shade of shrubs survived better than those in open spaces. This survivorship pattern is similar to that reported for other cactus species with different life-forms (e.g., globose and barrel cactus). Different kinds of perennial plants, such as agaves, grasses, trees, shrubs, and even cacti could decrease direct solar radiation and soil temperature, increasing the soil water availability for seed germination and seedling survival (Godínez-Alvarez et al., 2003). With respect to seed predation, birds, ants, and rodents are likely the main consumers of cactus seeds, and they negatively affect the establishment of individuals. Predation intensity could vary depending upon whether seeds are located beneath shrubs or in open spaces (Hutto et al., 1986; Sosa and Fleming, 2002). The results obtained during 2003 showed that seeds of *S. stellatus* that were not excluded from predators were rapidly removed by ants regardless of the site where they were located (i.e., beneath shrubs and open spaces). Similar findings have been reported for other species of columnar cacti, such as *Carnegiea gigantea*, *Neobuxbaumia*

a)



b)

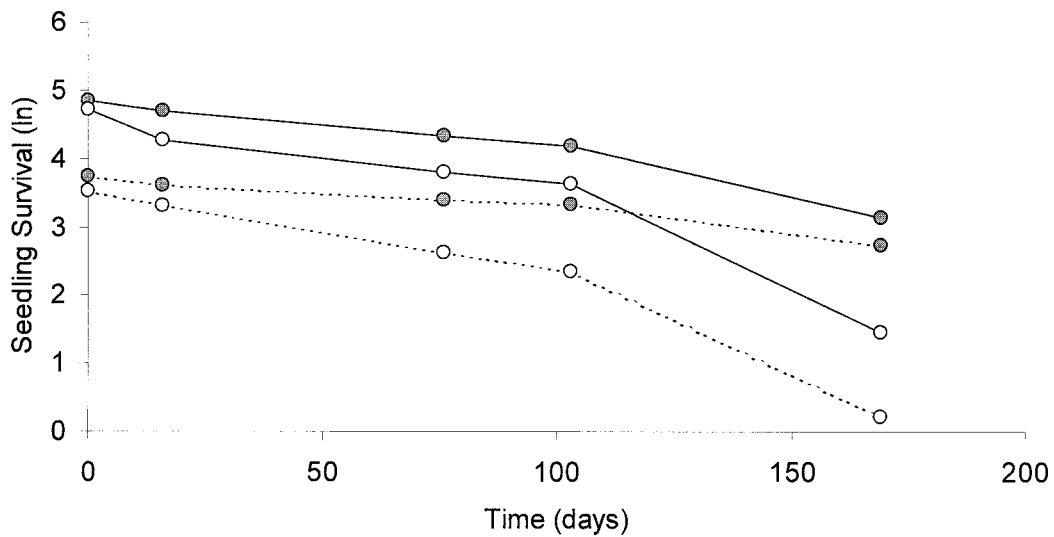


FIG. 1—Seed germination (a) and seedling survivorship (b) of *Stenocereus stellatus* in the Tehuacán Valley, Mexico. Closed and open circles refer to seeds and seedlings from Zapotitlán and Tilapa, respectively. In (b), seedlings were growing in open spaces (dashed line) or under the canopy of the shrub *Mimosa luisana* (line).

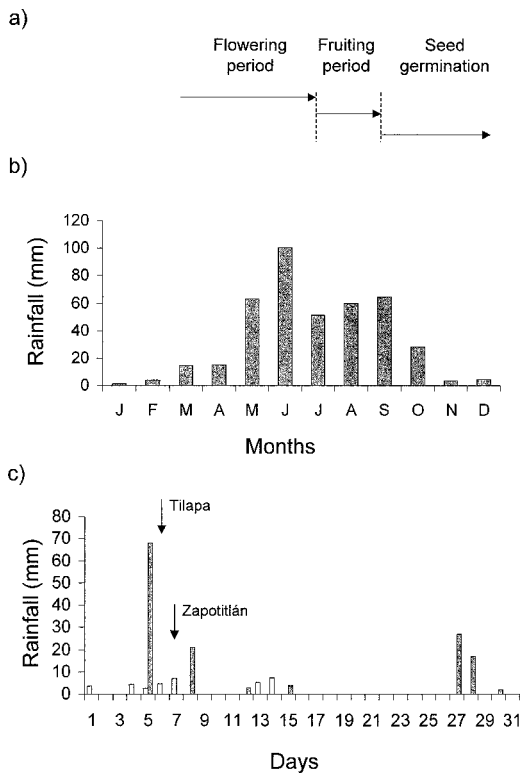


FIG. 2—Reproductive phenology of *Stenocereus stellatus* (a) and precipitation (b, c) in the Tehuacán Valley, Mexico. Part (b) refers to the mean monthly rainfall for a period of 30 years, and part (c) represents the rainfall pattern in Zapotitlán (closed bars) and Tilapa (open bars) during September 2003. The arrows indicate when the experiments of seedling establishment started in each site.

tetetz, *Pachycereus pringlei*, and *Stenocereus thurberi*, where seed predation did not significantly differ among distinct microhabitats (Valiente-Banuet and Ezcurra, 1991; Sosa and Fleming, 2002).

The amount and temporal distribution of rainfall might influence seedling emergence of *S. stellatus* under natural conditions. The seedling emergence failure of *S. stellatus* during 2003 might be related to insufficient amounts of rainfall to trigger seed germination. Steenberg and Lowe (1969) found that 2 or more precipitation events ranging from 21 to 82 mm within a period of 5 days were necessary to observe the seedling emergence of *C. gigantea* in Saguaro National Monument. Assuming that seeds of *S. stellatus* have similar water require-

ments to germinate, examining precipitation data at Zapotitlán and Tilapa showed that after the experiment was set up, the rainfall events were generally separated by more than 4 days and rainfall amounts tended to be less than 20 mm. The occurrence of periods with favorable conditions of rainfall is essential for the recruitment of individuals to the populations of different species of cactus (*Ferocactus acanthodes*, Jordan and Nobel, 1981; *F. cylindraceus*, Bowers, 1997; *C. gigantea*, Pierson and Turner, 1998).

Based on our results and the reproductive phenology of *S. stellatus* (Fig. 2a), favorable periods of rainfall seem critical for the establishment of sexually produced individuals. In the Tehuacán Valley, the rainfall pattern is bimodal with one peak occurring in June and the other in September, with the amount of rainfall higher in June (Fig. 2b). Seeds of *S. stellatus* mature during September, which might limit the probability of germination and seedling establishment; after September, the amount and frequency of rainfall decreases significantly. Due to this uncertainty associated with rainfall and seedling establishment, the ability of *S. stellatus* to propagate vegetatively might be viewed as a complementary mechanism (to sexual reproduction) that contributes to its population persistence. However, it remains necessary to conduct field studies to determine the variation in the number of recruits derived through vegetative propagation and sexual reproduction among years with different rainfall regimes.

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INLAND OCCURRENCE OF THE STRAND PLANT *IPOMOEA PES-CAPRAE* (CONVOLVULACEAE) AROUND LAKE NICARAGUA

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ABSTRACT—*Ipomoea pes-caprae* (L.) Roth (railroad vine, Convolvulaceae) is a pantropical, perennial beach plant that forms large patches just above the high tide line on coastal beaches and dunes throughout tropical and subtropical areas of the world. In spite of its wide distribution, only rare occurrences of *I. pes-caprae* have been documented in inland habitats. Here we report on an extensive population of *I. pes-caprae* growing on the shores of Lake Nicaragua in the interior of Nicaragua.

RESUMEN—*Ipomoea pes-caprae* (L.) Roth (la riñonina, Convolvulaceae) es una planta perenne y pantropical que forma parches grandes arriba de la línea de la marea alta en playas costeras y en dunas en áreas tropicales y subtropicales del mundo. A pesar de su amplia distribución, *I. pes-*

caprae ha sido documentado rara vez en hábitats tierra adentro. Aquí informamos de una población extensa de *I. pes-caprae* habitando la orilla del Lago Nicaragua en el interior de Nicaragua.

Ipomoea pes-caprae (L.) Roth (railroad vine, Convolvulaceae) is a pantropical perennial beach plant with showy, pink flowers and water-dispersed seeds. The plant possesses a self-incompatibility mechanism, although it is a pioneer species (Martin, 1970; Devall and Thien, 1989). *Ipomoea pes-caprae* forms patches just above the high-tide line on coastal beaches and dunes throughout tropical and subtropical areas of the world. The size of a patch varies depending on whether the beach is accreting or eroding, the recency and intensity of storms, and human activity. *Ipomoea pes-caprae* is one of the most widely distributed beach plants (Ridley, 1930) and is often a component of the strand (Austin and Weise, 1972; Porter, 1973; Whitten et al, 1984; Moreno-Casasola and Espejel, 1986; Devall, 1992). The primary pollinators of *I. pes-caprae* are bees, although butterflies, moths, flies, beetles, wasps, and ants also visit the flowers (Devall and Thien, 1989). Seeds of *I. pes-caprae* often are parasitized by the beetle *Megacerus leucospilus* (Bruchidae) (Teran and Kingsolver, 1977).

Ipomoea pes-caprae occurs on the coastal beaches of 5 continents and most tropical islands, as well as on warm temperate shores (St. John, 1970). In spite of its wide distribution, only rare occurrences of *I. pes-caprae* in inland habitats have been documented (Guppy, 1906; St. John, 1970; Austin, 1982; Austin and Cavalcante, 1982). Here we report on an extensive population of *I. pes-caprae* growing on the shores of Lake Nicaragua in the interior of Nicaragua, also listed in Taylor (1963) and Austin (2001).

Lake Nicaragua is 8,000 km² in area, with a mean elevation of 25 m, and has a total dissolved solid content of 0.07%, mostly sodium bicarbonate (Taylor, 1963). Sandy beaches are common on the western and northern shore of the lake, and the southern shore is rocky. We sampled the beach along Lake Nicaragua near the town of Malacatoya (Fig. 1) in November 1997 and October 1998 and in the city of Granada in October 2000. The sandy beach near Malacatoya is approximately 15 m wide and slopes down toward the water. In Granada,

there are a low seawall and a narrow sandy beach with occasional large rocks.

We studied *I. pes-caprae* on the shore of Lake Nicaragua following the methods of Devall and Thien (1989). We placed 15 1-m² quadrats 5 m apart along a transect that paralleled the beach, beginning near the front of the population (close to the water). The exact location of the first quadrat along the transect was randomly chosen by drawing a number. Two other transects were located parallel to the first, with 5 m between each transect. *Ipomoea pes-caprae* stems root adventitiously, and the extent of an individual plant cannot be easily determined, so we counted stems longer than 30 cm in length to determine density. Within each quadrat, we counted flowers, fruits, and seedlings. We also collected *I. pes-caprae* seeds at Malacatoya, stored them in plastic bags, and checked for bruchid (*Megacerus*) beetle larvae.

Thick mats of *I. pes-caprae* occur almost continuously from Granada to Malacatoya. The plants grow from the upper boundary of the beach to the high tide line. Other species in this area include water hyacinth (*Eichhornia crassipes* (Martins) Solms), pennywort (*Hydrocotyle bonariensis* Lam.), and water lettuce (*Pistia stratioides* L.). Beyond the beach are grasses. In June 2002, *I. pes-caprae* colonies occurred on the beach at the village of Sapoá, in disturbed areas, and at Cárdenas and Colón on the south shore of the lake, in patches at the high tide line. The species was present along the rocky shores of some small islands in the lake near Granada, with abundant water hyacinth surrounding the shores, and on San Fernando and small islands in the Solentiname archipelago. *Ipomoea pes-caprae* also grew at the ferry landing at San Jorge near Rivas and in the town of Moyogalpa on the large island of Ometepe.

Mean stem density of the *I. pes-caprae* patch at Malacatoya was 16.6/m² (Table 1). Mean flower density was 3/m², and mean fruit density was 4.3/m². No seedlings were observed in the quadrats. *Megacerus leucospilus* parasitized 9.9% of *I. pes-caprae* seeds ($n = 344$). There were fewer stems, flowers, and fruits in quadrats along transects at Granada, but a few seed-



FIG. 1—Map of Nicaragua showing Lake Nicaragua, the city of Granada, and other locations where *Ipomoea pes-caprae* was observed. Copyright Enchanted Learning. Used by permission.

TABLE 1—Mean (\pm SD) stem, flower, fruit, and seedling density (number per m²) of *Ipomoea pes-caprae* on the northern shore of Lake Nicaragua. Data were collected from 45 1-m² quadrats (each location) at Malacatoya in October of 1998 and from Granada in October of 2000. Flower data from around the Gulf of Mexico after Devall (1987); stem, fruit, and seedling density after Devall and Thien (1989).

Location	Stem density	Flower density	Fruit density	Seedlings
Malacatoya, Nicaragua	16.6 (7.6)	3.0 (3.3)	4.3 (5.6)	0
Granada, Nicaragua	7.8 (7.3)	0.4 (1.1)	4.1 (9.1)	0.2 (0.6)
Progreso, Yucatan, Mexico	5.8 (3.6)	0.4 (0.7)	3.5 (8.1)	0*
S. Padre Island, Texas, USA	3.6 (4.1)	2.0 (4.5)	0.3 (0.5)	0
Grand Isle, Louisiana, USA	0.6 (1.4)	0.5 (1.2)	1.6 (5.1)	0
Uaymitun, Yucatan, Mexico	6.4 (5.7)	0.1 (0.3)	0	0
San Bruno, Yucatan, Mexico	5.4 (4.5)	0	0	0

* One seedling was sampled.

lings were noted (Table 1). The stem densities of *I. pes-caprae* at Malacatoya and Granada were greater than that at 5 coastal locations around the Gulf of Mexico (Devall and Thien, 1989), where the mean stem density ranged from 0.6 to 5.8/m² (Table 1). We suggest the density of *I. pes-caprae* stems was greater around Lake Nicaragua because the plants were more protected from storms and hurricanes than are coastal populations. Herbivory of *I. pes-caprae* in populations around the Gulf of Mexico is slight, and the species tolerates human disturbance (Devall, 1987). Fruit density was also greater at Malacatoya (4.3/m²) compared to 0–3.5/m² around the Gulf of Mexico. No seedlings were found at Malacatoya or at 4 of 5 locations around the Gulf of Mexico (Devall and Thien, 1989); in contrast, a few seedlings (0.2/m²) were present at Granada. *Megacerus leucospilus* were found in 0.5–16% of seeds around the Gulf of Mexico, with more southerly populations exhibiting greater percentages of parasitized seeds; the rate was 9.9% at Malacatoya.

The occurrence of this large inland population of *I. pes-caprae* is unusual. *Ipomoea pes-caprae* is a widely distributed colonizing strand species on tropical beaches throughout the world (Sauer, 1959, 1967; St. John, 1970; Austin and Cavalcante, 1982; Fang and Staples, 1995; Austin, 2001). It has reached nearly all the locations at which it occurs by drifting of its seeds in the sea (Ridley, 1930). The species also occurs on the back margins of beaches, along coastal roads (Wilson, 1977), and in coastal villages, where it is dispersed by transportation of sand. It does not naturally invade inland habitats (St. John, 1970). Ridley (1930) stated that *I. pes-caprae* is never found inland, unless temporarily, after the seeds have been carried in sand. The landward extent of the species is limited by dispersal, competition, and shading by plants beyond the strand (Devall, 1992).

It was formerly thought that Lake Nicaragua and Lake Managua were formed when a large bay was cut off from the Pacific Ocean by volcanic activity (Hayes, 1899). Today it is thought that the Nicaraguan depression, including the 2 lakes, is a graben formed by subsidence during the late Tertiary and Quaternary (Thorson et al., 1966) or during the late Miocene (McBirney and Williams, 1965; Morris et al.,

1990). Mann et al. (1990) considered it a Quaternary structural depression that subsided as an asymmetric half graben along boundary faults on its southwestern side. It seems that the lakes were never connected to the Pacific.

For about 100 years after its founding in 1524, Granada was a thriving seaport for ships of up to 120 tons that traveled up the San Juan River, which connects Lake Nicaragua with the Caribbean. After that time, changes in the riverbed, as well as Dutch and English pirates, made the passage of large ships impossible, but small vessels continued to use the river to reach Granada (Carr, 1953).

A shark (*Carcharhinus leucas*), as well as sawfish and tarpon (all marine species), occur in the freshwater of Lake Nicaragua and the San Juan River. Thorson (1971) demonstrated that the sharks swim back and forth from the Caribbean to the lake along the river. The river, however, flows from the lake to the Caribbean (approximately 175 km), drops about 393 m, and contains several sections with named rapids. Because *I. pes-caprae* seeds did not float up the river, we suggest that the seeds were inadvertently carried up the river on ships traveling to Granada, perhaps as early as the 1500s, or were carried inland even earlier, given that the plant has been used medicinally for thousands of years. Water hyacinth, pennywort, and water lettuce are all non-natives and known “hitchhikers”, but all 3 are medicinal, so purposeful introductions around Lake Nicaragua cannot be excluded. We have not observed birds eating *I. pes-caprae* seeds, which contain ergot alkaloids (Jirawongse et al., 1979), but this would not preclude birds from eating them if the birds did not break the seed coats. It is possible that seeds were carried on the feet or feathers of birds that were wet or muddy. *Megacerus leucospilus* could have arrived in parasitized seeds along with viable seeds. The extensive spread of the plant around the lake indicates that it has been present for some time.

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SEASONAL MOVEMENT PATTERNS OF PICKEREL FROGS (*RANA PALUSTRIS*) IN AN OZARK CAVE AND TROPHIC IMPLICATIONS SUPPORTED BY STABLE ISOTOPE EVIDENCE

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ABSTRACT—We monitored a population of pickerel frogs (*Rana palustris*) in an Ozark cave over a 2-year period. Frogs were found from August to April with densities peaking from November to December. Although densities were quite high in these peak months, stomach content and stable isotope analyses reveal that *R. palustris* does not play a significant role as a predator in this subterranean system. These results suggest that the caves are being used as thermal refugia during the coldest months of the year.

RESUMEN—Observamos durante un periodo de dos años una población de *Rana palustris* en una cueva en los Ozarks. Se detectaron ranas de agosto y abril con densidades picos en noviembre y diciembre. Aunque las densidades fueron muy altas en estos dos meses, los contenidos estomacales y análisis de isótopos estables revelan que *R. palustris* no juega un papel significativo como depredador en este sistema subterráneo. Estos resultados sugieren que las cuevas son usadas como refugios térmicos durante los meses más fríos del año.

The North American continent is the richest in obligate cave-dwelling (troglotic) salamanders with approximately 10 described species, and possibly as many undescribed species, particularly from the Edward's Plateau, Texas. However, no troglotic anurans are known from this continent nor from temperate regions in general (Resetarits and Aldridge, 1988). Of the Nearctic anurans that inhabit caves opportunistically (troglonexes), frogs of the genus *Rana* are the most common (Barr, 1953; Prather and Briggler, 2001), especially the pickerel frog, *Rana palustris* (Myers, 1958; Schaaf and Smith, 1970; Black, 1971; McDaniel and Gardener, 1977; Resetarits 1986; Resetarits and Aldridge, 1988; Black and Sievert, 1989; Trauth et al., 2004). Seasonal use of caves by pickerel frogs has been attributed to avoidance of summer heat and drought and associated desiccation (Barr, 1953; Prather and Briggler, 2001), as well as avoidance of winter frost and related mortality (Resetarits, 1986; Resetarits and Aldridge, 1988). Pickerel frogs are so prevalent in Ozark caves that researchers originally hypothesized that their life cycle might be

completed underground (Brown, 1984). Hypotheses suggested that some demes might be evolving towards a body form specialized for subterranean existence (troglomorphy), although no evidence for modification of body form or of decreased reproductive output has been demonstrated in *R. palustris* (Resetarits and Aldridge, 1988). However, populations of *R. palustris* could impact true troglotic species through predation or competition. We investigated the potential seasonal use and trophic impact of a deme of pickerel frogs in an Ozark cave stream using a combination of field observations, stomach content analyses, and stable isotope assays.

We examined a population of pickerel frogs in January-Stansberry Cave, Delaware County, Oklahoma, located 6 km north of the town of Colcord. January-Stansberry Cave is a typical Ozark cave formed from the dissolution of fractures in Mississippian-aged, cherty limestone bedrock of the Boone Formation. The study area was defined as a 440-m section of the cave system (total mapped passage is approximately 1,800 m), beginning with the cave

mouth, where the subterranean stream "January River" resurges, and ending in the "Moonshine Room". The average passage dimensions are 5 m wide and 2 m tall. Terrestrial habitats within the cave include mud banks, cobble, bedrock, ceiling breakdown, precipitating formations (speleothems), and bat guano piles (ranging from 3 to 7 m in diameter and 0.1 m to 2 m in depth). A maternity population of approximately 15,000 gray bats (*Myotis grisescens*) inhabits the cave from April to October (pers. comm., S. Hensley, United States Fish and Wildlife Service). January River has an average depth of 1.0 m, but some pools are as deep as 2 m and riffles as shallow as 2 cm. The predominant substrate is chert cobble, but other substrate materials include clastic sediment and bedrock. Outside of the cave, January River flows 300 m as a surface stream until it joins Spavinaw Creek, a tributary of the Neosho River.

From July 2001 to October 2003, we performed monthly ocular censuses of pickerel frogs by using bright dive lights and helmet-mounted lamps; behavioral observations of frogs were recorded on diving slates. We grouped population counts by season (Winter: January, February, March; Spring: April, May, June; Summer: July, August, September; and Fall: October, November, December) and also grouped by cold period (winter and fall) and hot period (spring and summer). We employed a Chi-square test to test the null hypothesis that counts of pickerel frogs were evenly distributed by season and by period.

At the end of the study, we collected 32 adult pickerel frogs from within the cave and immediately preserved them for stomach content analysis following McDiarmid (1994). We had also conducted inventories in the cave ecosystem over 3 years and were confident that we could identify all common members of the fauna in the cave that could serve as potential food items for the frogs. We then dissected the stomachs of the frog and examined the contents under a stereomicroscope, identifying items to the lowest possible taxon; all contents were stored in glass vials in 95% ethanol. All specimens of frogs were deposited in the Sam Noble Oklahoma Museum of Natural History (catalog number OMNH 39837-68).

We employed natural abundance stable isotope analyses to elucidate the role of the pick-

erel frogs in the trophic web of January-Stansberry Cave. Isotope ratio mass spectrometry can detect small (one part per thousand) but predictable changes in ratios of carbon and nitrogen stable isotopes as organisms are assimilated into subsequent trophic levels (Gearing, 1991). An organism can be linked to its diet by the similarity of stable carbon isotope ratios ($^{13}\text{C}/^{12}\text{C}$), and the trophic position of an organism can be inferred by the characteristic enrichment of the stable nitrogen isotope ($^{15}\text{N}/^{14}\text{N}$) of 3.5‰ per trophic level (DeNiro and Epstein, 1981). In January 2003, we collected the following samples in triplicate as described in Graening and Brown (2003): leg muscle tissue of pickerel frogs, *M. grisescens* guano (feces), cave stream sediment, abdominal muscle of ringed crayfish (*Orconectes neglectus*), whole bodies of grotto salamander larvae (*Eurycea spelaeus*), composite samples of whole troglotic amphipods (*Stygobromus*) and isopods (*Caecidotea*), and one sample each of the whole body of cave salamander (*Eurycea lucifuga*) and dark-sided salamander (*E. longicauda melanopleura*). We collected animals under Oklahoma Department of Wildlife Conservation special license number 3086 and University of Oklahoma Animal Care and Use Committee assurance number A3240-01. We collected all samples in sterile glass vials with Teflon lids and immediately froze them for transport to the university lab. We then pulverized, freeze-dried, and sieved the samples through a number 30-mesh screen and had them analyzed at the Stable Isotope Ratio Facility for Environmental Research, University of Utah, Salt Lake City, using primary standards (Lajtha and Michener, 1994); analytical variability averaged 0.1‰.

Results of the monthly population censuses are presented in Fig. 1. Statistical analysis of the data revealed that counts of pickerel frogs were significantly different by season, with fall having the highest count and winter the second highest (Pearson $\chi^2 = 415.62$, $df = 3$, $P < 0.0001$). Pickerel frog counts also were significantly different by period, with the cold period (winter and spring) having higher counts (Pearson $\chi^2 = 232.67$, $df = 1$, $P < 0.0001$). Our field observations did not document any feeding activity by pickerel frogs. Of the 32 pickerel frogs collected for stomach content analysis, 14 had empty stomachs. We recovered stomach

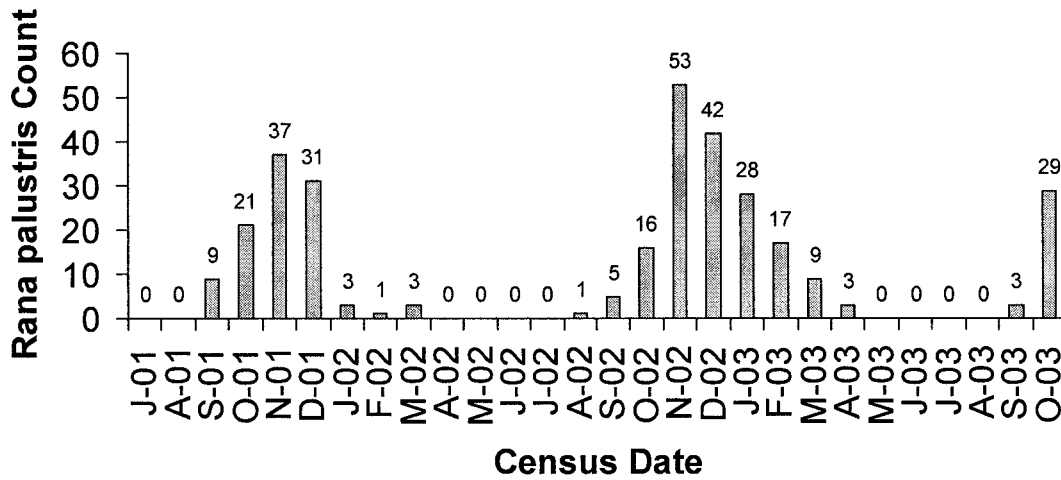


FIG. 1—Monthly ocular censuses of pickerel frogs (*Rana palustris*) in January-Stansberry Cave, Oklahoma, from July 2001 to October 2003.

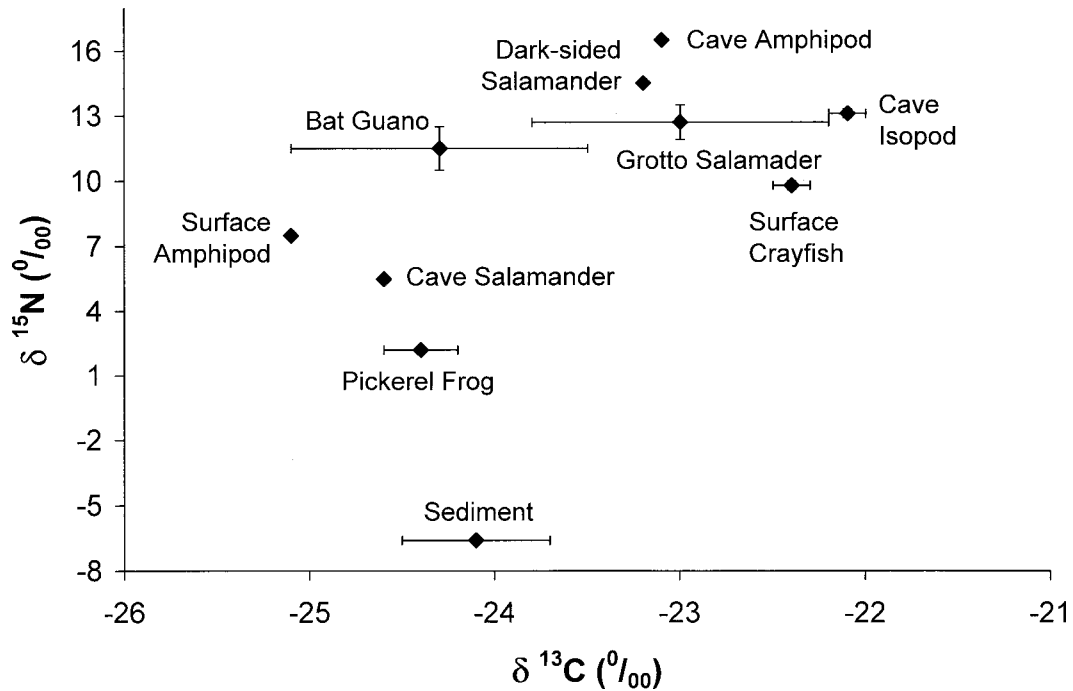


FIG. 2—Carbon and nitrogen stable isotope crossplot of pickerel frogs and their potential dietary items sampled on 12 January 2003 in January-Stansberry Cave, Oklahoma, replicated (*n*) as follows: cave sediment (*n* = 3); pickerel frogs (*Rana palustris*, *n* = 3); grotto salamander (*Eurycea spelaeus*, *n* = 4); cave salamander (*E. lucifuga*, *n* = 1); dark-sided salamander (*E. longicauda melanopleura*, *n* = 1); surface stream amphipods (*Gammarus*, *n* = 1); surface crayfish (*Orconectes neglectus*, *n* = 3); troglotic amphipods (*Stygobromus*, *n* = 2); isopods (*Caecidotea*, *n* = 3), and bat guano (*Myotis grisescens* feces, *n* = 3). Error bars are 1 *SD*. Nitrogen content of 2 cave sediment samples was below detection levels.

TABLE 1—Other occurrences of pickerel frogs (*Rana palustris*) in Ozark caves during cold months (G. Graening and M. Slay, unpublished data).

State, county	Site	Date	Count	
Arkansas				
Benton	Bear Hollow Cave	1 Oct 1999	1	
		6 Nov 2000	1	
Independence	Blevins' Cave	5 Oct 2002	1	
		Dozen's Den Cave	22 Mar 2001	1
Izard	Mr. Griffin's Cave	22 Nov 2002	5	
Marion	Blue Heaven Cave	23 Oct 2000	2	
Newton	Fitton Spring Cave	5 Oct 2000	1	
		Flowstone Façade Cave	5 Oct 2000	7
		Pretty Clean Cave	16 Mar 2002	1
		Tweet's Cave	26 Oct 2001	3
Stone	Flittering Pit	24 Nov 2002	5	
		Gunner Cave	27 Jan 2001	1
		Martin Hollow Cave	14 Oct 2000	4
		Unnamed cave	31 Mar 2002	1
Oklahoma				
Ottawa	Schifleff Cave	6 Dec 2003	1	
Delaware	Engelbrecht Cave	8 Dec 2003	1	
Sequoyah	Cottonwood Cave	9 Dec 2003	1	

contents in various states of digestion, making specific identification difficult. We were able to make the following taxonomic delineations: 6 Diptera (including 2 Heleomyzidae), 13 Arthropoda (including 5 Coleoptera), and 2 plant tissues.

Results of stable carbon and nitrogen isotope analyses, presented as a dual isotope crossplot (Fig. 2), graphically demonstrate that the isotopic signatures of the pickerel frogs sampled differ from the other animals inhabiting the cave. If pickerel frogs were consuming these potential prey items, such as crustaceans or salamanders, the position of the frogs in the crossplot should be higher (i.e., the nitrogen isotopic signature of the frog tissues should be enriched in ^{15}N).

Contrary to the most recent study of pickerel frogs in Ozark caves (Prather and Briggler, 2001), our study documented a population of pickerel frogs that used an Ozark cave during the winter season, and not summer. In a concurrent bioinventory of other caves in the Ozark Plateaus Ecoregion, we found pickerel frogs during fall and winter months in at least 16 other caves, summarized in Table 1. Resetarits (1986) reported that pickerel frogs were most abundant in caves in winter. We concluded

that populations of pickerel frogs use caves in the Ozarks to avoid harsh conditions in summer or in winter, but not necessarily both, and local site conditions apparently dictate the period of use. The derivation of this apparent behavioral thermoregulation is not known, but Dowling (1956) and Resetarits (1986) hypothesized that it is a relictual behavior derived from the use of caves as refugia from climatic extremes of Pleistocene glacial advance and retreat.

The persistence of ranid populations in caves might have significant impact upon subterranean ecosystems, both in terms of energy flow and community composition. Temperate subterranean ecosystems are generally energy poor environments, and frogs might contribute energy via their feces and cadavers (Culver, 1982; Resetarits, 1986). More importantly, perhaps, is their potential role as predators. Bullfrogs (*Rana catesbeiana*) inhabiting caves have been reported to consume subterranean organisms, including troglobitic salamanders (*Gyrinophilus palleucus*) and crayfish (*Procambarus lucifugus*), and at least 3 species of bats (Lee, 1969; Kirkpatrick, 1982). Smith (1948) documented the stream isopod *Lirceus hoppinae* to be a regular prey item of the pickerel frog.

Yet our analyses suggest that the pickerel frog population in January-Stansberry Cave was not preying upon the other trophic members in our study cave; nearly half of all frogs collected for the stomach content analysis had nothing in their stomachs at all. We believe that the pickerel frog is not a significant threat to Ozark subterranean communities, unlike the voracious bullfrog.

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PRELIMINARY ASSESSMENT OF THE DIET OF *GYALOPION*
QUADRANGULARE (SERPENTES: COLUBRIDAE)

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ABSTRACT—We describe the diet of the thornscrub hook-nosed snake (*Gyalopion quadrangulare*) using prey remains removed from the alimentary tracts of museum specimens. Diet consisted of small arthropods, including 9 (31%) insects, 9 (31%) spiders, 8 (28%) scorpions, and 3 (10%) that could not be identified further. Insects included 7 orthopterans (both crickets and grasshoppers) and 2 that we could not identify further. We identified half of the scorpions as *Diplocentrus spitzeri*. Prey class frequencies are dependent on geographic distribution, but independent of sample source (stomach vs. intestine/feces). Snakes that ate different prey classes did not differ significantly in snout-vent length.

RESUMEN—Describimos la dieta de la culebra de naricilla del desierto (*Gyalopion cuadrangulare*) usando restos de presas extraídos de tractos digestivos de especímenes en museos. La dieta consiste de pequeños artrópodos incluyendo 9 (31%) insectos, 9 (31%) arañas, 8 (28%) escorpiones, y 3 (10%) que no pudieron ser identificados. Los insectos incluyeron 7 ortópteros (grillos y saltamontes) y 2 que no pudieron ser identificados. Identificamos la mitad de los escorpiones como *Diplocentrus spitzeri*. Las frecuencias de clase de presa son dependientes de la distribución geográfica, pero independientes de la fuente de muestreo (estómago vs. intestino/heces). Las serpientes que consumieron diferentes clases de presas no difirieron significativamente en la longitud hocico-cloaca.

Thornscrub hook-nosed snake (*Gyalopion quadrangulare*) was described in 1885 (Gunter, 1885–1902) and was first documented in the United States less than 50 years ago (Woodin, 1962). Its distribution ranges northward from Nayarit, Mexico (between the coast and the Sierra Madre Occidental) into Santa Cruz County, Arizona (Stebbins, 2003). In Arizona, it inhabits mesquite grassland and Madrean oak woodlands between 1,000 and 1,402 m elevation. In Mexico, *G. quadrangulare* inhabits creosote shrublands, thorn-scrub, thorn-forest, dry tropical forest, and subtropical forest communities (Stebbins, 2003). Information regarding the diet of this small (up to ca. 300 mm total length), seemingly secretive species is confined to anecdotal observations reported in the literature. Woodin (1962) reported spiders from 2 wild-caught specimens and fed captive snakes spiders and a small centipede. Bogert and Oliver (1945) noted spiders in the stomachs of 3 specimens from Sonora, Mexico, and

Hardy (1975) reported a scorpion from the stomach of a museum specimen (LACM 6841). Fowlie (1965:42) suggested that *G. quadrangulare* are probably “wholly insectivorous (and spider eating).” Rossi and Rossi (2003:165) reported spiders as “its favorite food” and noted that captive snakes ate spiders, crickets, and scorpions. Most field guides (Behler and King, 1979; Bartlett and Tenant 2000; Stebbins, 2003) suggest the diet includes spiders, centipedes, and scorpions, though Bartlett and Tenant (2000) suggested that insects probably are consumed also.

We examined the stomach and posterior 3 cm of the intestine of 50 specimens of *G. quadrangulare* in the Arizona State University (ASU) and University of Arizona (UAZ) collections (Appendix I) for prey remains. Specimens were collected from the states of Sonora ($n = 23$), Arizona ($n = 16$), Sinaloa ($n = 8$), Nayarit ($n = 2$), and one from an unknown locality in Mexico. We omitted prey from specimens

TABLE 1—Prey consumed by thornscrub hook-nosed snakes (*Gyalopion quadrangulare*) in this study, exclusive of 3 unidentified arthropods, and including prey records originally reported by Woodin (1962) that we also examined.

Prey taxon	Northern populations	Southern populations	Total
Arachnida	3 (43%)	6 (32%)	9 (35%)
Insecta	0 (0%)	9 (47%)	9 (35%)
Unidentified insect	0	2	2
Orthoptera	0	7	7
Scorpionidae	4 (57%)	4 (21%)	8 (30%)
Unidentified scorpion	0	4	4
<i>Diplocentrus spitzeri</i>	4	0	4
Total	7	19	26

housed in captivity prior to preservation or those that apparently were fed in captivity (allopatric or domestic prey). We identified scorpion remains to the greatest taxonomic resolution possible using a reference collection (G. L. Bradley). We identified spiders and insects to the greatest resolution possible from exoskeletal remnants of chelicerae, leg, body segments, or combinations of these structures.

For statistical analyses, we grouped prey into 3 classes (spiders, insects, scorpions) and disregarded the 3 arthropods that could not be identified further. To assess geographic variation, we divided samples into northern and southern groups. The southern group included all samples that contained prey remains collected from Alamos (Sonora, Mexico) or farther south in thornscrub habitats. The northern group included samples from the United States (ca. 230 km north of Alamos) collected from mesquite-oak savannah and associated riparian habitats. We computed statistics using BIOMstat version 3.3 (Exeter Software, Setauket, New York). Means are reported ± 1 SD, and significance level was set at $\alpha = 0.05$.

Twenty-six (52%) of 50 *G. quadrangulare* specimens contained 29 identifiable prey; 19 identified from intestinal contents and 10 from stomach contents. Diet consisted of 9 (31%) insects, 9 (31%) spiders, and 8 (28%) scorpions (Table 1); 3 (10%) additional samples contained arthropod remains that could not be identified further. Insects included 7 orthopterans (both crickets and grasshoppers) and 2 unidentified insects. Half of the scorpions were specifically identified as *Diplocentrus spitzeri*, all of which were removed from specimens col-

lected in the Pajarito Mountains, Arizona. We detected multiple prey in 3 specimens (spider + orthopteran + unidentified insect; spider + scorpion; scorpion + scorpion). The specimen containing 2 scorpions had eaten 2 large adult *D. spitzeri*.

Prey class was dependent on geographic group (R \times C test of independence, $G_{\text{Williams}} = 7.0$, $df = 2$, $P = 0.03$, $n = 26$), with the northern group containing a higher proportion of scorpions and no insects. Prey class was independent of the sample source (stomach vs. intestine; R \times C test of independence, $G_{\text{Williams}} = 3.6$, $df = 2$, $P = 0.17$, $n = 26$). The 3 samples containing arthropod remains (that could not be assigned to a prey class) were taken from the intestines of snakes collected in Sonora and Sinaloa. Snakes that ate spiders were shorter on average (198 ± 29 mm snout-vent length = SVL) than those that ate scorpions (227 ± 28 mm SVL) and insects (227 ± 41 mm SVL). However, SVL did not differ significantly among prey classes (ANOVA, $F_{(2,23)} = 2.3$, $P = 0.12$). Although there was a trend for scorpion and spider consumption later in the year (relative to insects), date of collection did not differ significantly among prey classes (Kruskal-Wallis, $H = 5.6$, $n = 25$, $P = 0.06$). Only 5 prey (17%) were recovered from females: 1 insect (Orthoptera), 2 spiders, and 2 unidentifiable arthropods.

Most general works suggest *G. quadrangulare* diet consists of spiders, scorpions, crickets, and centipedes (Bogert and Oliver, 1945; Woodin, 1962; Bartlett and Tennant, 2000; Ernst and Ernst, 2003; Rossi and Rossi, 2003; Stebbins, 2003), and several of these authors suggested

that spiders dominate the diet. Our limited dataset suggested that spiders, scorpions, and insects occur in approximately equal proportions in *G. quadrangulare* diet. Although centipedes are listed frequently as prey in field guides, we found no definitive evidence, in the literature or among the specimens we examined, of predation in the wild on centipedes. The speculation about centipede consumption in the wild appears to be based on the observation by Woodin (1962) of a captive eating a small centipede. However, occasional consumption of centipedes does not seem unlikely given the presence of centipedes in the diets of many other members of the Sonorini and the abundance of centipedes in many of the habitats occupied by *G. quadrangulare*. Interestingly, all identifiable scorpion remains were *D. spitzeri*, despite the presence of at least 4 other sympatric scorpion species at the collection locality (Pajarito Mountains, Arizona). Two of these species (*Vaejovis spinigerus* and *Centruroides exilicauda*) exhibit high population densities in this area. *Diplocentrus spitzeri*, like *G. quadrangulare*, is at its northern distributional limits in southern Arizona. This might suggest similar microhabitat affinities for both species in the northern portions of their distributions. Data presented here suggest that *G. quadrangulare* diet might vary geographically. Although small sample size precludes authoritative inferences, the complete absence of insects from northern populations is notable, given their prevalence in the southern sample.

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APPENDIX 1—*Specimens Examined*—ASU 4734, 6236, 6288, 6392, 6656, 6665, 6713, 8227, 13617, 23212, 27395, 31495–96, 33284, 33391; UAZ 16294, 20733–34, 20814, 24926, 31420, 36445–47, 36563, 37678, 37710–11, 37741, 39233–34, 39558–563, 42850, 42908, 43676, 43920, 45197, 45906, 46151, 46668–69, 47352, 48253, 48341, 55550.

REPRODUCTION OF THE PLAINS POCKET GOPHER
(*GEOMYS BURSARIUS*) AND BAIRD'S POCKET GOPHER
(*G. BREVICEPS*) IN TEXAS

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ABSTRACT—We examined large series of the plains pocket gopher (*Geomys bursarius*) and Baird's pocket gopher (*G. breviceps*) collected in every month of the year in 10 Texas counties. Based on lengths of testes, both species potentially reproduce in every month of the year, although the likelihood of reproduction decreases in summer and autumn. Data from females revealed that breeding actually begins in late December or early January and continues through October (in Baird's pocket gopher) or November (in the plains pocket gopher).

RESUMEN—Examinamos una amplia serie de la tuza de pradera (*Geomys bursarius*) y de la tuza de Baird (*Geomys breviceps*), colectadas cada mes del año en diez condados de Texas. Basado en la longitud de los testículos, ambas especies potencialmente se reproducen cada mes del año aunque la probabilidad de reproducción disminuye en el verano y el otoño. Datos de las hembras revelaron que el apareamiento comienza a fines de diciembre o a los inicios de enero, y continúa a lo largo de octubre (en el caso de la tuza de Baird) o a través de noviembre (en el caso de la tuza de pradera).

The plains pocket gopher, *Geomys bursarius*, is an autochthonous Great Plains species that ranges southward from Manitoba into Texas (Jones et al., 1985). In the South, its distribution is surrounded by those of 6 cryptic relatives, of which 4 are virtually indistinguishable from *G. bursarius* and were recognized as distinct species only after genetic analyses (Honeycutt and Schmidly, 1979; Block and Zimmerman, 1991; Burt and Dowler, 1999). One of those cryptic species is Baird's pocket gopher, *Geomys breviceps*, which occurs in prairie habitats and oak savannas in eastern Texas, southeastern Oklahoma, and adjacent areas of Arkansas and Louisiana (Honeycutt and Schmidly, 1979).

Baird's pocket gopher was regarded as a subspecies of the plains pocket gopher until it was discovered that the taxa differ both chromosomally and genically (Bohlin and Zimmerman, 1982; Cothran and Zimmerman, 1985; Dowler, 1989; Block and Zimmerman, 1999). The 2 species hybridize occasionally, but there is limited gene exchange between them (Coth-

ran and Zimmerman, 1985; Dowler, 1989). Because the plains pocket gopher and Baird's pocket gopher are related and similar, we hypothesized that complex phenomena, such as those associated with reproduction, are identical or nearly so, especially near areas where the 2 species are parapatric. In this regard, most of what is known about reproduction in Baird's pocket gopher is based on a study done in the vicinity of College Station, Texas (Wood, 1949). Two comprehensive studies on reproduction in the plains pocket gopher have been conducted, but both studies were located to the north, in Colorado (Vaughan, 1962) and Missouri (Pitts and Choate, 1997). Accordingly, it was not known whether information from previous studies on the plains pocket gopher could be used for comparison with the limited reproductive data available for Baird's pocket gopher.

In Missouri, breeding by plains pocket gophers has been documented from late December through June (Pitts and Choate, 1997). In Colorado, this gopher breeds from late Feb-

ruary through August (Vaughan, 1962). Baird's pocket gopher reportedly begins breeding no earlier than February and continues through August (Wood, 1949; Schmidly, 1983). However, we trapped a Baird's pocket gopher with obviously swollen uterine horns on 31 December 1988, and 1 of 4 females that we trapped on 21 January 1989 was pregnant. We thus became suspicious that Baird's pocket gopher reproduces throughout winter, like the plains pocket gopher does in Missouri. We therefore investigated the annual cycle of reproduction in both the plains pocket gopher and Baird's pocket gopher near their geographic zone of contact in Texas.

We used Victor traps to collect pocket gophers at various locations in 10 Texas counties (Brazos, Cooke, Denton, Grayson, Grimes, Henderson, Lamar, Madison, Montague, and Wise) in every month of the year. Fieldwork began in December of 1988 and ended in September of 2004. All pocket gophers were dissected, their reproductive condition was ascertained, and voucher specimens were deposited in either the Sternberg Museum of Natural History at Fort Hays State University, Hays, Kansas, or the Texas Cooperative Wildlife Collection at Texas A&M University, College Station. Identification of specimens trapped near the zone of contact between the 2 species was confirmed by means of karyotypes ($2n = 72$ in *G. bursarius*; $2n = 74$ in *G. breviceps*) or mtDNA sequences (J. Bickham, pers. comm.; Pitts et al., 1999).

We assigned gopher specimens to age categories based on reproductive condition and, when necessary, external size. We regarded males with testes longer than 3 mm as adults except in August and September, when a few large adults had testes just 3 mm in length. We regarded those large individuals as adults based on their total lengths, which exceeded 215 mm in plains pocket gophers and 210 mm in Baird's pocket gophers. We assumed that females in which the pubic symphysis had been absorbed were past puberty (Hisaw, 1924). We recognized those individuals as adults except in November and December, when pubic symphysis were being absorbed in a few relatively small females. We regarded those small individuals as subadults based on their total lengths, which were less than 200 mm for both species. We classified males and females of both species

as juveniles if they were distinctly small and immature.

We interpreted testis size, pregnancy, lactation, and the presence of obvious juveniles as indications of reproduction. In plains pocket gophers, testes longer than 12.5 mm generally contain spermatozoa, whereas testes shorter than about 12 mm generally do not (Vaughan, 1962). Likewise, in Baird's pocket gophers, testes measuring more than 11 mm reportedly have large epididymides and contain spermatozoa (Wood, 1949; Sulentic et al., 1991). However, the presence of spermatozoa means only that reproduction is possible, not that it occurs. We thus used testis size as a measure of reproductive potential rather than reproductive activity and recorded the cyclic change in lengths of testes in all months of the year in both species. Likewise, for both species we recorded the dates and incidence of pregnancy, lactation, and the presence of obvious juveniles. We regarded these as evidence of actual reproduction.

We collected 1,469 pocket gophers for this study. This included 691 plains pocket gophers (238 adult males, 35 subadult males, 4 juvenile males, 381 adult females, 24 subadult females, and 9 juvenile females) and 778 Baird's pocket gophers (306 adult males, 25 subadult males, 2 juvenile males, 420 adult females, 21 subadult females, and 4 juvenile females) (Table 1). Thus, 60% of the plains pocket gophers trapped were females, as compared with 62% in Missouri (Pitts and Choate, 1997) and 57% in Colorado (Vaughan, 1962). For Baird's pocket gopher, 57% of the animals caught were females. Landowners encouraged us to trap out the local populations of pocket gophers, and in most instances, we attempted to do so. Therefore, we assume that the disparity of females to males represents actual female gender bias rather than differential trappability of males and females. No previous study has ascertained the extent of the female gender bias in Baird's pocket gopher. Numbers of both species of each sex and age category trapped in each month are shown in Table 1.

Monthly mean lengths of the right testes in the plains pocket gopher and Baird's pocket gopher in Texas are presented in Table 1. In both species, size of testes suggested that males potentially could reproduce in every month al-

TABLE 1—Specimens of *Geomys bursarius* and *Geomys breviceps* collected in Texas each month of the year sorted by age, gender, and reproductive condition.

Month	Males					Females					
	Adult males (<i>n</i>)	Testes lengths (range)	Testes lengths (mean)	Subadult males (<i>n</i>)	Juvenile males (<i>n</i>)	Adult females (<i>n</i>)	Number pregnant (<i>n</i>)	Percentage pregnant	Number lactating (<i>n</i>)	Subadult females (<i>n</i>)	Juvenile females (<i>n</i>)
<i>G. bursarius</i>											
January	14	10–21	16.1	1	0	24	2	8.33	0	0	0
February	19	15–20	17.4	0	0	29	7	24.14	0	0	0
March	10	12–18	16.9	1	0	30	17	56.67	7	0	1
April	41	5–20	15.9	4	2	63	22	34.92	10	2	4
May	25	5–19	15.0	6	0	28	8	28.57	8	1	1
June	17	5–18	14.2	6	1	33	6	18.18	6	7	0
July	10	3–12	8.3	3	0	19	4	21.05	4	4	2
August	16	3–18	7.5	2	0	15	2	13.33	0	1	0
September	27	3–15	6.6	7	1	32	1	3.13	1	4	0
October	23	3–16	8.9	2	0	36	0	0	0	3	0
November	19	4–17	13.5	2	0	49	1	2.04	0	0	1
December	17	11–18	13.9	1	0	23	0	0	0	2	0
Total	238			35	4	381	70	18.42	36	24	9
<i>G. breviceps</i>											
January	19	11–19	15.8	1	0	30	1	3.33	0	2	0
February	27	16–19	16.4	0	0	47	25	53.19	0	0	0
March	57	12–18	16.1	1	0	55	25	45.45	10	1	0
April	19	13–20	15.8	1	0	33	7	21.21	14	0	1
May	19	8–17	13.3	4	1	27	5	18.52	14	5	0
June	19	8–15	11.6	5	1	22	3	13.64	8	1	0
July	12	3–14	9.1	2	0	13	3	23.08	2	2	0
August	12	3–12	6.9	0	0	14	0	0	0	1	0
September	19	3–12	6.7	6	0	14	0	0	1	0	1
October	37	3–15	7.8	4	0	54	1	1.85	0	3	1
November	14	6–18	11.2	1	0	30	0	0	1	0	0
December	52	8–19	14.7	0	0	81	0	0	5	6	1
Total	306			25	2	420	70	17.77	55	21	4

though the likelihood of reproduction decreases in summer and autumn.

Reproductive data recorded from female pocket gophers (Table 1) were more informative than were those from males. The earliest evidence of reproduction in the plains pocket gopher was a female captured on 22 January that contained 3 fetuses and another female captured on 23 January that contained 2 fetuses. We subsequently trapped pregnant plains pocket gophers in every month through September and again in November, with the highest incidence of pregnancies occurring from February through August (Table 1). March was the only month in which more than half of all adult female plains pocket gophers trapped were pregnant. We captured lactating plains pocket gophers from March through July and in September, and juvenile plains pocket gophers from March through July and in September and November (Table 1). Seventy pregnant female plains pocket gophers contained from 1 to 5 fetuses (average 2.53). This is a smaller average litter size than reported previously for Colorado (3.4) and Missouri (3.14) (Vaughan, 1962; Pitts and Choate, 1997).

The earliest evidence of reproduction in Baird's pocket gopher was the female captured on 21 January that contained 3 fetuses (Pitts et al., 1992). We subsequently trapped pregnant Baird's pocket gophers in every month through July and again in October, with most pregnancies occurring from February through July (Table 1). Approximately half of all adult female Baird's pocket gophers trapped in February and March were pregnant. We captured lactating Baird's pocket gophers from March through July and in September, October, and December, and juvenile Baird's pocket gophers from April through June and in September, November, and December. Sixty-six pregnant female Baird's pocket gophers contained from 1 to 5 fetuses (average 2.51). This is just slightly less than the average litter size (2.6) reported previously for this species (Wood, 1949).

If it can be assumed that pocket gophers with testes containing spermatozoa are capable of breeding (Vaughan, 1962; Sulentic et al., 1991), then our data indicated that males of these 2 pocket gopher species are capable of breeding in Texas essentially throughout the year, although the likelihood of reproduction

decreases in summer and autumn. In this respect, the annual cycle of monthly mean lengths of testes (Table 1) corresponds closely with those reported by Vaughan (1962) and Pitts and Choate (1997). Data from female plains pocket gophers, however, showed that they evidently do not become receptive in Texas until late December or early January, and they subsequently breed until October, with the last pregnancies occurring in November. We concluded from these data that the breeding season for the plains pocket gopher in Texas is longer than it is in Colorado or Missouri. In Baird's pocket gopher, females become receptive in December and breed until September, with the last pregnancies in October.

Results of this study indicated that the reproductive patterns of plains and Baird's pocket gophers are essentially identical near their zone of parapatry. In fact, the patterns of these 2 species are more similar than are those of northern and southern populations of the plains pocket gopher. The fact that the pattern varies more with latitude than between species suggests that reproductive cycles in these subterranean rodents might be regulated by climate, possibly through its effects on vegetation consumed by pocket gophers. However, too little is known about either seasonal or latitudinal variation in the diets of pocket gophers to attempt to explain why reproduction would essentially cease in autumn and resume in winter.

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USE OF COASTAL WETLANDS BY HISPID COTTON RATS (*SIGMODON HISPIDUS*)

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ABSTRACT—Hispid cotton rats (*Sigmodon hispidus*) occur primarily in grass-dominated habitats. These habitats abut tidal wetlands along the Gulf and Atlantic coasts of the United States occupied by the marsh rice rat (*Oryzomys palustris*). Few data document whether cotton rats also occupy wetlands and whether interspecific interactions exist with rice rats. We used livetraps to sample 4 grids that each encompassed wetland and upland habitats near Galveston, Texas. Cotton rats occurred in both upland and wetland habitats. Density of cotton rats was lower in wetlands; their residence time was less in wetlands, which perhaps indicated poorer survival or movement to uplands. Sex ratio, proportion reproductive, and age structure, however, did not differ between upland and wetland habitats. Density of cotton rats and rice rats was negatively correlated. Such density compensation coupled with differences in diel activity and diet minimizes potential for interspecific competition.

RESUMEN—La rata algodonera crespa (*Sigmodon hispidus*) se encuentra mayormente en hábitat dominada por hierba. Estos hábitat terminan en pantanos afectados por marea a lo largo de las costas del Golfo y del Atlántico de los Estados Unidos. Los pantanos están ocupados por la rata arrocera de pantano (*Oryzomys palustris*). Pocos datos documentan si las ratas algodoneras también habitan pantanos y si existen interacciones interespecíficas con ratas-arroceras. Utilizamos trampas para obtener muestras de 4 cuadrículas que incluyeron hábitat pantanosas y de tierra alta cerca de Galveston, Texas. Las ratas algodoneras habitaban tanto áreas de tierra alta como áreas pantanosas. La densidad de las ratas algodoneras en áreas pantanosas fue más baja; su tiempo de residencia en áreas pantanosas fue menor, lo que quizá indica menor sobrevivencia o traslado a

tierra alta. La proporción de los sexos, la proporción reproductiva, y la estructura de edad, sin embargo, no difirieron en hábitats de áreas pantanosas y de tierra alta. La densidad de la rata algodónera y la rata arrocera de pantano se correlacionaron negativamente. Tal compensación de densidad junto con diferencias en actividad en períodos de veinticuatro horas y dieta minimiza la posibilidad de competencia entre especies.

Sympatric species can minimize interspecific interactions by occupying different habitats within the same geographic region or by selecting different microhabitats within the same habitat (Kelt et al., 1995; Brown et al., 2002; Eccard and Ylonen, 2003). The hispid cotton rat (*Sigmodon hispidus*) and marsh rice rat (*Oryzomys palustris*) occur sympatrically in south-central and southeastern USA. Both species occupy grass-dominated habitats, but hispid cotton rats occupy upland prairie (Cameron and Spencer, 1981), while marsh rice rats prefer wetlands (Wolfe, 1982). Low occurrence of cotton rats in wetlands has been reported (Andre, 1981; Wolfe, 1985), and marsh rice rats and cotton rats might co-occur in ecotones between uplands and wetlands, particularly during dry seasons (Pournell, 1950; Birkenholz, 1963; Goertz and Long, 1973).

In low-lying habitats subject to seasonal flooding, hispid cotton rats and marsh rice rats use separate microhabitats. For example, marsh rice rats occupied poorly drained areas dominated by dicots, while hispid cotton rats preferred drier upland prairie dominated by monocots in coastal prairie of Texas (Kincaid et al., 1983). In Everglades of Florida, marsh rice rats and hispid cotton rats occupied habitat on the edge of tropical hardwood hammocks, while the cotton mouse (*Peromyscus gossypinus*) occupied hammock centers during the wet season. In the dry season, hispid cotton rats occupied prairie between hammocks, the cotton mouse occurred on hammocks, and marsh rice rats moved to mesic sites (Smith and Vrieze, 1979; Smith, 1980). A lack of complementarity in density between marsh rice rats and hispid cotton rats led Smith (1980) to conclude that interspecific interactions were not important.

In numerous places along rivers and the Gulf and Atlantic coasts, upland habitat dominated by grasses such as *Andropogon*, *Trypsacum*, and *Schizachyrium* grades into fresh or tidal wetlands dominated by *Typha* or *Spartina*. In such areas along the Texas coast, Kruckek

(2004) discovered that marsh rice rats used upland coastal prairie adjacent to tidal marshes during winter and spring as dispersal sinks and as refuges during high tides. Hispid cotton rats also occurred in this upland prairie, suggesting the possibility of interspecific interactions. We measured occupancy of upland and wetland habitats by hispid cotton rats in this same Texas habitat. We tested the hypothesis that hispid cotton rats used wetland habitat seasonally as a dispersal sink and evaluated the potential for interspecific interactions between hispid cotton rats and marsh rice rats.

Our research was conducted at 4 field sites located along Galveston Bay, Texas, from January through December 1997. Two field sites were at Galveston Island State Park (29°12'17"N, 94°57'58"W) and 2 sites were along Highland Bayou (20°10'34"N, 94°56'16"W). Vegetation at all sites included: *Spartina alterniflora* (smooth cordgrass) in low marsh; *Batis maritima* (saltwort), *Monanthochloë littoralis* (salt-flat grass), *Salicornia bigelovii* (annual glasswort), *S. virginica* (perennial glasswort), and *Borrchia frutescens* (sea ox-eye daisy) in mid-marsh; and, *Spartina spartinae* (Gulf cordgrass), *Schizachyrium scoparium* (little bluestem grass), and *Baccharis halimifolia* (sea-myrtle; Correll and Johnston, 1970) in upland coastal prairie.

A trapping grid at each site extended from low marsh into upland coastal prairie. Grids covered 1.76 ha (195 × 90 m) and 1.82 ha (135 × 135 m) at Galveston Island State Park and 2.34 ha (195 × 120 m) and 2.16 ha (180 × 120 m) along Highland Bayou. Grid size varied because of different configurations of marsh and upland habitats at each site.

Sherman live-traps (7.8 × 9.3 × 23.5 cm) were placed 15 m apart in equal numbers in each habitat. Traps in wetland were held on platforms (45 × 20 cm) of expanded polystyrene with bungee cords that kept them afloat during periods of high water. Trap platforms were nestled into vegetation to prevent them from floating away. Traps were baited with birdseed and an apple slice just before sunset

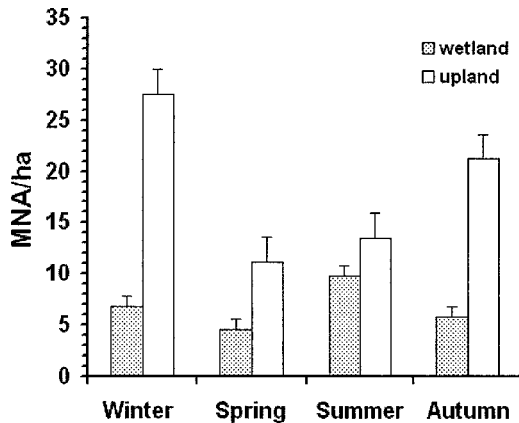


FIG. 1—Average density (Minimum Number Alive/ha) of *Sigmodon hispidus* in upland and wetland habitat along Galveston Bay, Texas, during winter (January to March), spring (April to June), summer (July to September), and autumn (October to December). Error bars depict + SE.

and were checked at sunrise for 3 days each month. Species, sex, reproductive condition (determined by descended testes and by perforate vagina, enlarged nipples, or pregnancy), and body mass were recorded for each captured animal. Animals were individually marked with an eartag and toeclip, and were released at their capture location.

Abundance (Minimum Number Alive [MNA]; Krebs, 1999), age structure (percent juvenile [0 to 59.9 g], subadult [60 to 109.9 g], and adult [≥ 110 g]; Cameron, 1977), sex ratio (percent males), and reproductive activity (percent males and females that exhibited reproductive traits) were computed. Density was computed for each habitat type by using MNA in that habitat type and dividing by half of grid area; other demographic variables also were determined separately for each habitat type. Because of low captures during some months, data were grouped into seasons (winter, January through March; spring, April through June; summer, July through September; and autumn, October through December; Cameron, 1977). Demographic parameters were analyzed by 2-way repeated-measures analysis of variance (ANOVA) using season and habitat (wetland, upland) as factors, and trapping grids as replicates. Variables expressed as percentages were normalized with an arcsine transformation (Zar, 1999). Simple correlation

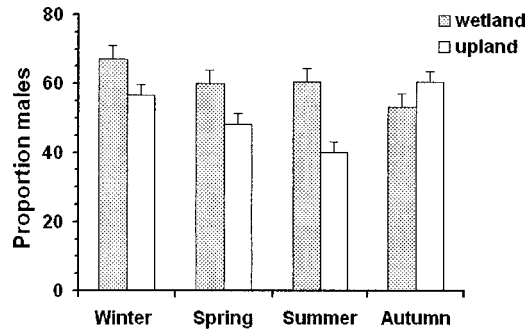


FIG. 2—Sex ratio of *Sigmodon hispidus* as shown by percentage of males in upland and wetland habitats along Galveston Bay, Texas. Seasons as in Fig. 1. Error bars depict + SE.

analysis was used to investigate the relationship between monthly density of hispid cotton rats and marsh rice rats (data on rice rats from Kruchek, 2004). Data are presented as mean \pm SE.

There was a habitat-by-season interaction of density ($F = 5.4$, $df = 3, 18$, $P < 0.01$) because density of cotton rats increased in uplands during autumn and winter, while density in wetlands remained relatively constant among seasons (Fig. 1). Density in wetland (8.11 ± 1.0 /ha) was less than density in upland (18.4 ± 2.4 /ha; $F = 13.9$, $df = 1, 6$, $P < 0.01$), and density was higher during autumn and winter than during spring and summer ($F = 5.2$, $df = 3, 18$, $P < 0.01$). Density of hispid cotton rats was negatively correlated with density of rice rats ($r = -0.45$, $df = 30$, $P < 0.01$; $n = 32$).

Overall sex ratio did not differ from equality ($60.2 \pm 4.0\%$ males in upland, $51.5 \pm 2.9\%$ males in upland; $\chi^2 = 15.3$, $df = 31$, $P = 0.99$; Fig. 2). Proportion of males did not differ between habitats ($F = 2.4$, $df = 1, 6$, $P = 0.17$) or among seasons ($F = 1.1$, $df = 3, 18$, $P = 0.37$). There was not a season-by-habitat interaction ($F = 1.5$, $df = 3, 18$, $P = 0.24$).

Proportion of reproductive males ($F = 7.2$, $df = 3, 18$, $P < 0.002$) and females ($F = 5.0$, $df = 3, 18$, $P < 0.01$) was higher during spring and summer than during autumn and winter (Fig. 3). There was no difference between habitats in proportion of reproductive males ($53.8 \pm 8.0\%$ in wetland, $44.3 \pm 7.3\%$ in upland; $F = 1.2$, $df = 1, 6$, $P = 0.31$) or females ($65.4 \pm 7.2\%$ in wetland, $76.1 \pm 3.7\%$ in upland; $F = 2.4$, $df = 1, 6$, $P = 0.18$). Proportion of the

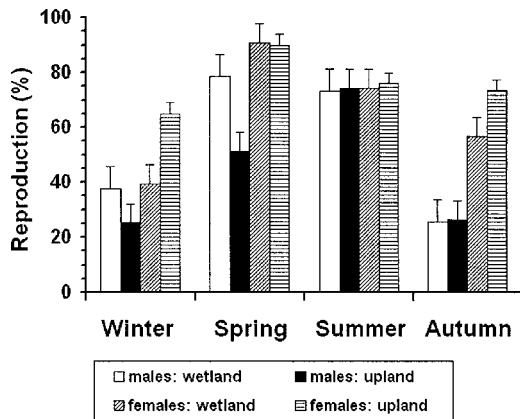


FIG. 3—Percentage of male and female *Sigmodon hispidus* that were reproductive in upland and wetland habitat along Galveston Bay, Texas. Seasons as in Fig. 1. Error bars depict + SE.

population that was reproductive did not have a season-by-habitat interaction for males ($F = 0.61$, $df = 3, 18$, $P = 0.62$) or females ($F = 0.71$, $df = 3, 18$, $P = 0.56$).

Adults were more abundant during winter and spring ($F = 8.4$, $df = 3, 18$, $P < 0.001$), subadults were more abundant during autumn ($F = 15.0$, $df = 3, 15$, $P < 0.001$), and juveniles were more abundant during summer ($F = 5.1$, $df = 3, 18$, $P < 0.01$; Fig. 4). There was no between-habitat difference in proportion of adults ($F = 1.4$, $df = 1, 6$, $P = 0.28$), subadults ($F = 0.93$, $df = 1, 6$, $P = 0.37$), or juveniles ($F = 0.02$, $df = 1, 6$, $P = 0.89$). There was no season-by-habitat interaction for adults ($F = 0.93$, $df = 3, 18$, $P = 0.45$), subadults ($F = 1.1$, $df = 3, 18$, $P = 0.37$), or juveniles ($F = 0.34$, $df = 3, 18$, $P = 0.80$).

Salt marshes in Galveston Bay are highly fragmented and arranged as isolated or semi-isolated habitat patches. Kruczek (2004) concluded that marsh rice rats existed as a metapopulation where local populations had some risk of extinction, but this risk could be spread among independently fluctuating local populations (Pulliam, 1996). Marsh rice rats used upland habitat in winter and spring as dispersal sinks and refuges from high tides and cold temperatures (Kruczek, 2004). The situation differed for hispid cotton rats. Coastal prairie along Galveston Bay is less fragmented than wetlands and hispid cotton rats have dispersal corridors among patches of coastal prairie. In

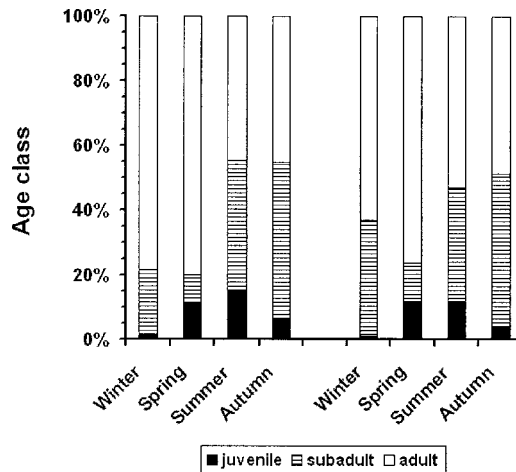


FIG. 4—Percentage of *Sigmodon hispidus* population that was adult, subadult, and juvenile in upland (left) and wetland (right) habitats along Galveston Bay, Texas. Seasons as in Fig. 1.

addition, the only demographic parameter of hispid cotton rats that differed between habitats was lower density in wetlands. If wetlands were used as dispersal sinks or refuges from abiotic factors, we would expect a skewed age distribution (e.g., higher proportion of subadults) or seasonal difference in density (e.g., increase during periods of high density in uplands) in wetlands. Neither of these results occurred, leading us to reject our hypothesis that hispid cotton rats used wetlands as dispersal sinks or refuges in the fashion that marsh rice rats used uplands.

Wetlands were used during all seasons by hispid cotton rats as additional habitat, although density was lower in wetlands. Periodic flooding of wetlands might lower the quality of this habitat for hispid cotton rats because they are less adapted for aquatic life than marsh rice rats, which are superior swimmers, have water-repellent fur, and can better maintain body-core temperature (Esher et al., 1978). Daily or seasonal flooding of wetlands might keep density of hispid cotton rats low, either because of higher mortality or movement to upland during periods of high water. Either of these causes is reflected by lower residence time in wetlands (number of recaptures/individual averaged 1.82 ± 0.11 in wetland and 2.43 ± 0.12 in upland; $F = 11.8$, $df = 1, 387$, $P < 0.001$).

In either case, demographic groups were affected equally.

Density complementarity between hispid cotton rats and marsh rice rats resulted from differences in timing of reproduction and population growth. Density of marsh rice rats was lowest in autumn and increased from winter through summer (Fig. 1 in Kruchek, 2004), whereas density of hispid cotton rats was lowest in spring and increased from summer through winter (Fig. 1). Juvenile marsh rice rats were most abundant during summer, followed by subadults in autumn, and adults in winter and spring (Fig. 4 in Kruchek, 2004). Juvenile hispid cotton rats were most abundant in spring and summer, followed by subadults in summer and autumn, and adults during winter and spring.

In addition to density complementarity, differences in daily activity and diets might minimize interspecific interactions. Activity of hispid cotton rats peaks immediately at dark, with a smaller peak later in the night, whereas activity of marsh rice rats occurs between peaks of hispid cotton rat activity (Kilduff and Dube, 1979). Marsh rice rats in these habitats eat primarily aquatic organisms and wetland vegetation in both upland and wetland, with upland plants accounting for <6% of diet items (Kruchek, 2004). On the other hand, >95% of diet of hispid cotton rats is comprised of upland plants (Kincaid and Cameron, 1982). Hence, in spite of habitat overlap between hispid cotton rats and marsh rice rats along Galveston Bay, complementarity in demography, differences in diel activity, and differences in diet would minimize interspecific interactions.

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DOCUMENTATION OF AN URBAN WINTER ROOST OF THE SPOTTED BAT (*EUDERMA MACULATUM*)

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ABSTRACT—We report the first documented use of a building as a winter roost by *Euderma maculatum*. We suggest that sufficient numbers of *E. maculatum* have been encountered in urban settings that researchers should consider these areas during the course of investigations of species occurrence. We recommend that urban settings in the vicinity of large cliff features be sampled systematically for the presence of *E. maculatum*.

RESUMEN—Reportamos el primer caso documentado del uso de edificios como refugio de invierno por *Euderma maculatum*. Sugerimos que han sido encontrados suficientes individuos de *E. maculatum* en asentamientos urbanos por lo que los investigadores deben considerar éstas áreas para los estudios enfocados a la presencia de especies. Recomendamos que los asentamientos urbanos cercanos a grandes acantilados deben ser muestreados para la presencia de *E. maculatum*.

The spotted bat (*Euderma maculatum*) was first described by Allen (1891) and is considered rare throughout its range, which is distributed over much of western North America from southern British Columbia into central Mexico (Hall, 1981; Poché, 1981; Leonard and Fenton, 1983; Fenton et al., 1987; Pierson and Rainey, 1998; Geluso, 2000). Only 35 specimens were recorded in the literature between 1890 and 1965 (Watkins, 1977), with 73 specimens catalogued by 1985 (Best, 1987). Technology has advanced in the area of survey equipment (e.g., acoustic recording devices, small radio-transmitters), allowing researchers to determine this species to be both more widely distributed and abundant than was previously supposed. For example, from only 14 known records of *E. maculatum* in California prior to 1991, Pierson and Rainey (1998) used acoustic sampling of potential foraging areas to add 23 new localities, representing both lat-

itudinal and elevational range extensions for the species.

Despite increased documentation of occurrence of *E. maculatum* throughout its range, it has been suggested that local occurrence is likely constrained to specific habitats that include large cliffs for roosting coupled with suitable habitats for foraging (Easterla, 1965, 1971; Findley, 1993). Pierson and Rainey (1998) described *E. maculatum* to be a near-obligate cliff-roosting species, with individuals rarely encountered ≥ 10 km from substantial cliffs. Rabe et al. (1998) reported that a lactating female *E. maculatum* routinely traveled 38.5 km (one way) between its day roost and foraging area. This certainly indicates that individuals are capable of moving relatively long distances, potentially taking advantage of foraging areas across a diversity of habitats and landscape scales. The reliance on a combination of non-randomly distributed roosting habitat and lo-

cally available foraging areas results in a patchy distribution of *E. maculatum* throughout its range (Pierson and Rainey, 1998; Geluso, 2000).

While documentation of warm-season activities continues to accumulate, the winter habits of this species remain unknown. Poché (1981) captured several *E. maculatum* in Fort Pierce Wash, Utah, during the winters of 1975 and 1976, but was unable to locate winter roosts for this species. Hall (1939) reported a discovery of an *E. maculatum* on a rock at a base of a cliff in Kern County, California, in December 1933, but was unsure if the location was an actual roost. In fact, the 2 most commonly cited reports (Hardy, 1941; Parker, 1952) for *E. maculatum* roosting in winter were from caves observed in 1930 and 1948 in Utah and California, respectively. Unfortunately, voucher specimens were either not collected or have been lost, diminishing these observations to anecdotal references. Furthermore, these second-hand accounts for cave roosts were not verified during our subsequent investigations (pers. obser., RES). Poché (1981) suggested that possible migration would be local, where animals seek refuge deep in humid cracks and crevices to hibernate.

Our community outreach practices of the Museum of Southwestern Biology lead to frequent exchanges with the public about roosting bats in homes and businesses. During one such dialogue with a business, we were able to secure data presented in this paper. Here we describe the first documented winter roost of *E. maculatum* and discuss potential impacts of these findings on management of this species.

In January 1997, employees of Sumo Medical Supply Company notified us that a bat was roosting in a warehouse in Albuquerque, Bernalillo County, New Mexico. Upon investigation, we were unable to locate roosting bats, although we located guano beneath the area where a bat had been observed by the employees. Species identification is critical for bat management recommendations (type and timing of exclusions, for instance) in buildings. We installed an acoustic detector (Anabat, Ballina, New South Wales, Australia) to record and collect echolocation calls, with which to identify species. During the first 4 nights of recording, we failed to detect echolocation calls, despite continued accumulation of guano be-

low the roosting area. We were unable to stay in the facility overnight because of reasons of security, so we recalibrated the acoustic equipment to facilitate detection of lower frequency calls and reset the recorder. That next night, we recorded calls consistent with those produced by *E. maculatum* (Fig. 1). We felt that this occurrence likely represented a transient individual that would likely soon leave. The bat vacated the warehouse and was neither observed nor recorded that year after 16 February 1997.

On 17 January 1998, we were notified that a bat had been observed again in the same area as the previous year. Acoustical calls consistent with those of *E. maculatum* were recorded in the same fashion as the year before through 21 February 1998. On 28 January 1999, a message from the warehouse informed us that a bat was flying inside of the building and had alighted near the office. We immediately went to the site to find that an employee had killed the bat. The animal was prepared as a dry study specimen (skin, skeleton, tissues), and catalogued (MSB 135536, NK 45594) into the Museum of Southwestern Biology, Division of Mammals. The *E. maculatum* proved to be a mature male (mass 9.1 g, total length 116 mm, length of tail 48 mm, length of right foot 12 mm, length of ear 42 mm, length of tragus 15.5 mm, length of forearm 53 mm, testes 2×5 mm). A comparison of MSB 135536 with an available range of measurements suggests that the bat we collected was fully developed, but slightly underweight at time of collection. Poché (1981) reported average mass of 11 male, wintering *E. maculatum* as 13.8 g, while Hall (1981) provided ranges for total length (107 to 115 mm), length of ear (37 to 47 mm), and length of forearm (48 to 51 mm).

We compared temperatures during periods immediately prior to and following site occupancy. We also compared temperatures in the 3 years following removal of the animal from the roost. Average temperatures during January and February and periods of roost occupancy were obtained from a nearby weather station (Albuquerque METAR). In 1997, average temperature during January and February was 2.6°C, while average temperature during roost occupancy was 3.8°C. In 1998, average 24-h temperature during January and February was 3.6°C, while average temperature during

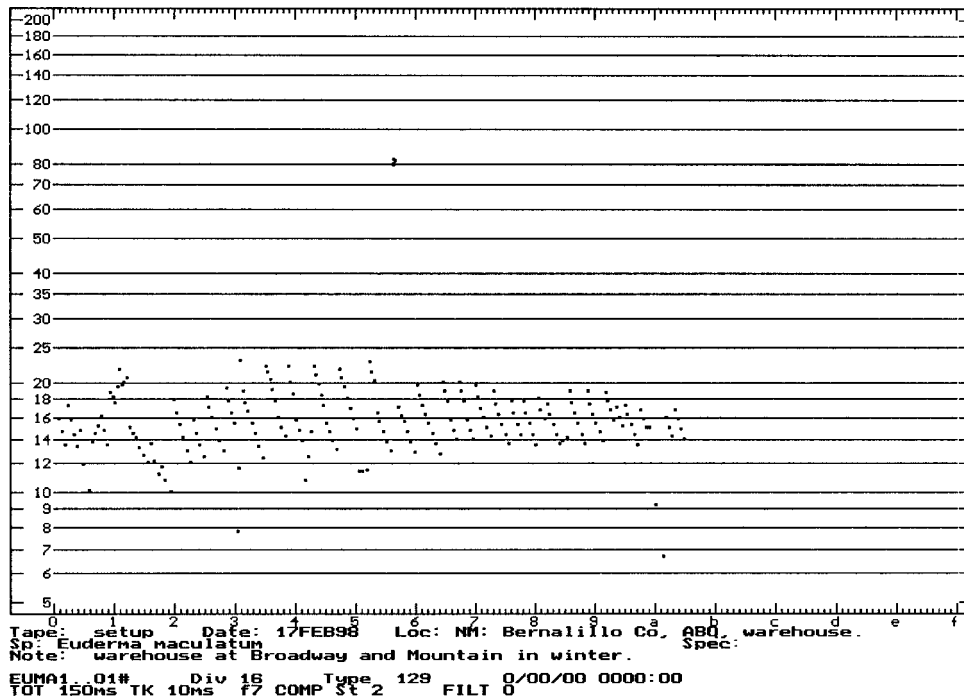


FIG. 1—Echolocation call of *Euderma maculatum* recorded 17 February 1998 from an Albuquerque, New Mexico, warehouse. Call sequences were recorded using Anabat detector, ZCAIM, and laptop computer set in monitor mode. Time is compressed and displayed where each time scale represents 150 ms.

roost occupancy was 4.1°C. In 1999, average temperature during January and February was 5.6°C, while average temperature during roost occupancy was 5.9°C. Average temperatures from January through February since 1999 were 6.1°C (2000), 3.3°C (2001), and 3.7°C (2002). We determined that temperatures were statistically similar among years ($F = 1.22$, $df = 176$, $P = 0.183$), during periods of roost occupancy, periods immediately prior to and following occupancy, and in the roosting periods in years following the removal of the roosting animal ($F = 1.85$, $df = 167$, $P = 0.175$).

We cannot state with certainty that it was the same individual roosting in the warehouse for each of the 3 successive years. However, the bat(s) seemed to use the same roosting area based on guano deposition and acoustical recordings each year. No individuals have been reported from the warehouse since the collection of this individual. Therefore, we assume that this was the same animal roosting in the warehouse each year. It would seem that this individual selected and reused this roost be-

cause it satisfied basic requirements of winter roosting over successive years. We found no correlation between anomalies in local ambient temperature and periods of occupancy of the structure by *E. maculatum*. However, the individual(s) encountered in the warehouse was routinely defecating, suggesting that some foraging was taking place during period of occupancy.

Winter activity in bats is not unusual at lower latitudes (O'Farrell and Bradley, 1970). Poché (1981) captured *E. maculatum* in mist nets when ambient air temperatures were as low as -5°C and speculated that winter activity of spotted bats was a reflection of increased need for water during the hibernation period. Average temperatures (24 h) recorded in Albuquerque during periods of roost occupancy (and periodic activity) were 3.8°C (1997), 4.1°C (1998), and 5.6°C (1999). These temperatures are sufficiently cool that insect abundance would be greatly diminished. However, some insects do remain active at cool temperatures (O'Farrell and Bradley, 1970) such that a va-

TABLE 1—Published anecdotal accounts of 24 roost sites for specimens of *Euderma maculatum* listed from oldest to most recent date of observation. Four observations (17%) were made in times other than summer (March through October), and 15 roosts (63%) were found in human-made structures.

Location	Date of observation	Literature source
Human-made roosting structures		
On fence, Castaic Creek, California	March 1890	Allen, 1891
In biological lab, Las Cruces, New Mexico	September 1903	Miller, 1903
On side of brush house, Yuma, Arizona	28 April 1904	Vorhis, 1935
In zoological lab at University of Nevada, Reno	10 September 1922	Hall, 1935
On side of building, under eaves, Yosemite Valley, California	17 August 1931	Ashcraft, 1932
In mine, Sonora, Mexico	Unknown	Vorhies, 1935*
Under eaves of high school, Salt Lake City, Utah	29 October 1934	Durrant, 1935
On side of porch, Twentynine Palms, California	May 1939	Bensen, 1954
On porch, St. George, Utah	Summer 1939	Hardy, 1941*
Oil field warehouse, Byron, Wyoming	27 August 1960	Mickey, 1961
Screen door, residence, Aztec, New Mexico	21 September 1960	Rodeck, 1961
Campus building, University of Nevada, Las Vegas	15 September 1961	Deacon and Bradley, 1962
On outside wall of house, Friant, California	6 June 1970	Medeiros and Heckmann, 1971
Albuquerque Public School Book Repository, New Mexico	November 1971	This paper
Warehouse, Albuquerque, New Mexico	February 1997, 1998, 1999	This paper
Natural roosting structures		
Crocodile Cave, Utah	4 February 1930	Hardy, 1941*
On lower side of rock at base of cliff, Kern County, California	December 1933	Hall, 1939
On rock projection in cave, near Pilot Knob, California	22 March 1948?	Parker, 1952*
Released bats flew to cracks and crevices in cliffs, Big Bend National Park, Texas	June to August 1969, June 1970, June 1971	Easterla, 1973
Crevice in cliff, Ft. Pierce Wash, Utah	May 1974	Poché, 1981
Cracks and crevices in cliff, Ft. Pierce Wash, Utah	June and July 1974, June and July 1976	Poché, 1975, 1981
Steep cliff (presumably in cracks), Okanogan Valley, British Columbia, Canada	May to August 1981	Leonard and Fenton, 1983
Cracks in ceiling of cave, Marble Canyon region, Arizona	May to October 1995 to 1997	Mead and Mikesic, 2001
Night roost in trees, Kaibab Plateau, Arizona	July 1996	Rabe et al., 1998

* Anecdotal, secondhand account

riety of species of bats are routinely active during the winter months. It also is possible that the animal was foraging in the warehouse where temperatures were maintained at room temperature, approximately 20°C.

This documented winter roost site for *E. maculatum* in a building was unexpected because this species is regarded as an obligate of cliff features associated with deep, relatively isolat-

ed canyons (Pierson and Rainey, 1998). Consequently, it is considered accidental in an urban setting (Easterla, 1971). However, the bat(s) used this warehouse for portions of 3 winters, which suggests use of buildings cannot be dismissed. In addition, the only other confirmed (but unpublished) *E. maculatum* roost in New Mexico is from the Albuquerque Public School Book Repository (collected in Novem-

ber 1971; MSB 32594). In fact, a surprising number of roosting *E. maculatum* have been found in human-made structures (Table 1), often in urban settings (Ashcraft, 1932; Durrant, 1935; Hall, 1935; Hardy, 1941; Bensen, 1954). Geluso (2000) reported that 35% (11) of all known occurrences of *E. maculatum* in Nevada are from buildings in either Reno or Las Vegas. In general, 33% of specimens (7 of 21) of *E. maculatum* collected prior to 2001 were collected in buildings in either rural or urban settings, and the described summer roosts from all but 2 locations are buildings (Table 1). Recently identified roosts of *E. maculatum* included a day roost in a cave (Mead and Mikesic, 2001) and night roosts in trees (Rabe et al., 1998). Both roosting areas included nearby cliff features, but use of these roosts certainly suggests more plasticity in roost choice than is generally acknowledged for this species (Easterla, 1973).

This observation of spotted bats at an urban, winter roost is intriguing when compared with historical collections of *E. maculatum*. The association of this bat with urban areas was acknowledged by Vorhies (1935:226), who stated that to increase likelihood of encountering *E. maculatum* “. . . others of us in the southwest might hopefully try leaving our windows open.” We suggest that sufficient numbers of *E. maculatum* have been encountered in urban settings and recommend that urban settings with nearby, large cliff features be sampled preferentially in surveys for the presence of *E. maculatum*.

We would like to thank the employees of Sumo Medical Supply for allowing us access to their facilities. We acknowledge and thank M. S. Burt for assistance in monitoring of the site, G. R. Racz and D. S. Tinnin for their comments on earlier drafts of this manuscript, and 2 anonymous reviewers for their thorough consideration of this paper. G. Suzan provided the resumen in Spanish. We especially thank all those who act on behalf of bats and science by contacting the University of New Mexico, Museum of Southwestern Biology with interesting natural history observations.

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